

BIOGEOGRAPHY OF THE ENDEMIC FRESHWATER FISH *CRATEROCEPHALUS* (FAMILY ATHERINIDAE)

L.E.L.M. CROWLEY

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Biogeography of the freshwater species of the atherinid genus *Craterocephalus* (hardyheads) is examined with reference to previous biogeographic studies of freshwater fish faunas in Australia and Papua New Guinea. A new hypothesis challenges the concept of recent speciation and suggests that there were two temporally separate invasions of ancestral types, giving rise to the two freshwater species groups of this genus. This hypothesis is supported by osteological work, which separates the freshwater hardyheads into two distinct lineages, and by the present distribution of hardyhead species in relation to the geologic history of Australia and Papua New Guinea.

□ *Atherinidae, Craterocephalus, biogeography, Australia, Papua New Guinea.*

L.E.L.M. Crowley, School of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia; 29 June, 1988.

Australia is notably lacking in diversity of freshwater fishes, and it seems that Talent (1984) was perfectly justified in commenting that the endemic fish fauna was dull when compared with that of Africa and South America. McDowall (1981) was also correct when he suggested that the lack of taxonomic work precluded any realistic appraisal of Australian fish biogeography, whereas Whitley (1959) was probably incorrect when he suggested that the endemic fauna was too recent in origin to have allowed significant radiation of species. In contrast, I suggest that the paucity of freshwater species may be due to other factors:

- i) the relative stability of much of the Australian continent throughout the Tertiary;
- ii) the general aridity of much of the continent since mid-Miocene;
- iii) the physiological adaptability of many of the smaller fish to changing habitats.

An additional factor, which does not account for the apparent paucity of freshwater fish but does contribute to statements such as those noted above, is the lack of taxonomic work.

TECTONIC STABILITY

The Australian mainland has been relatively stable since the Paleocene, apart from its continued northwards movement and Tertiary tectonism along the eastern and southern highland areas (Wellman, 1987). However, there have been marine transgressions (Lloyd, 1969; van de Graaff *et al.*,

1977; Veevers, 1984), the most recent of which separated Papua New Guinea from the Australian continent. During the Plio-Pleistocene there were also orogenies and epirogenies which resulted in river captures or changes in direction of river flow (Twidale, 1966; Heidecker, 1973; Maxwell, 1973; Hopley *et al.*, 1980), but these were restricted mainly to northern Queensland (Day *et al.*, 1983). During the last 60 million years, apart from Eastern Highland tectonics, there has been a lack of geological "vicariant events" in most of the continent, with concomitant lack of new habitats and, therefore, of speciation potential.

GENERAL ARIDITY

Australia is the second most arid continent in the world (Williams, 1984). Rainfall in Australia is seasonal and also very variable, with floods in some years and drought or near-drought in others. With such unpredictable rainfall, many freshwater habitats in central, northern and western regions of the continent are ephemeral and may have been so since the onset of aridity in the mid-Miocene (Bunting *et al.*, 1973; van de Graaff *et al.*, 1977; but see also Bowler *et al.*, 1976). Whilst such unpredictable conditions might be regarded as favouring speciation, ephemeral floodwaters allow dispersal of species and populations, both within and between river systems (Horn Scientific Expedition, 1896; Whitley, 1959; Glover & Sim, 1978a & b). During dry seasons populations retreat

<i>C. s. fulvus</i>
00100001101110010100010001000101011111111
<i>C. s. stercusmuscarum</i>
001000011011100101101010001000101000111011111111
<i>C. dalhousiensis</i>
0011111001110010101010000010001000000110111111001
<i>C. randi</i>
0010001111110010110010000010001010001110011111111
<i>C. nouhuysi</i>
0010000111110010110000100010101010001110100111001
<i>C. lacustris</i>
00100001011110011110000000010001010000110111111101
<i>C. knilghensis</i>
0001001111110010001000100010001010000000011111111
<i>C. cyrenii</i>
000000100100011010000000001010100001110111110000
<i>C. euneiceps</i>
00000010010011000010010100011000001001101011100010
<i>C. marjoriae</i>
0000001000000110100000100110001000001101111110010
<i>C. marianae</i>
0000001000000110100000011011101010001100111110001
<i>C. helenae</i>
000100110000111010010101011110111001110011110001
<i>C. katloiae</i>
0000001000010110000001010001110100011100000010111
<i>C. honorius</i>
110101010100010100010110000001010001000111111111
<i>C. pauciradiatus</i>
001101110010000110101110001011110000100111111110
<i>C. capreoli</i>
000111111100011110101100011100010000110011111110
<i>C. mugiloides</i>
110101011010001011101001010010100001100111111101

to refuge areas, some of which may be fed by natural springs. Other freshwaters may disappear completely during times of prolonged drought, so that their inhabitants perish. Dispersal with the onset of rain allows interbreeding between surviving, but previously isolated, populations (Glover, 1982). Floods occur frequently enough to ensure that the genetic integrity of species is maintained (see, for example, Russell, 1892; Simpson & Douth, 1977; Allen *et al.*, 1986). So, present aridity and the vagaries of the climate cannot be considered as "vicariant events".

PHYSIOLOGICAL ADAPTABILITY

Habitats in Australia are frequently variable as a result of the climatic conditions. In dry seasons

TABLE 1. Fifty-one characters (in order) used in the binary analysis based on an algorithm of Sneath and Sokal (1973). For each, positive statement = 1; negative = 0.

1. vomerine teeth, present/absent; 2. mesopterygoid teeth, present/absent; 3. 5th ceratobranchial, fused/unfused; 4. premaxillary teeth, restricted to front of jaw/not restricted; 5. dentary teeth, restricted/not restricted; 6. premaxillary teeth, visible externally/not visible; 7. anterior dentary, broad/narrow; 8. interdorsal pterygiophores, well developed/vestigial or absent; 9. mesopterygoid, large/small; 10. base premaxilla, broad/narrow; 11. urohyal ventral pocket, present/absent; 12. urohyal ventral wings, present/absent; 13. posterior notch of coracoid, large/small; 14. scapular foramen, large/small; 15. ventral flange of 5th ceratobranchial, large (high)/small (low); 16. ventral flange of 5th ceratobranchial, elongate/short; 17. lateral process terminal half centrum, long/short; 18. basal process parhypural, large/small; 19. posterior pterotic process, long/short; 20. posterior basibranchial toothplate, present/absent; 21. toothplates on 2 & 3 ceratohyals, present/absent; 22. toothplates on all hypobranchials, present/absent; 23. epibranchial toothplates on 2, 3 & 4, present/absent; 24. 1st ceratobranchial toothplates, present/absent; 25. mesethmoid, present/absent; 26. long teeth on anterior of 5th ceratobranchial; present/absent; 27. supraoccipital crest, large/small; 28. dermosphenotic, broad/narrow; 29. quadrate, very large/small; 30. metapterygoid, large/small; 31. Zary process premaxilla large/small or absent; 32. anterior projection of coronoid, present/absent; 33. haemal arches of caudal vertebrae, curved/straight; 34. palatine, pointed/cylindrical; 35. palatine-nasal ligament, long/short; 36. antero-medial part of nasal deeply recurved/not deeply recurved; 37. ventral anterior process of nasal for attachment of palatine-nasal ligament, strongly hooked/not hooked; 38. neural plate of 2nd vertebra, large/small; 39. cleithrum anterior projection, present/absent; 40. supracleithrum, long, slender/short, broad; 41. infraorbital canal, open/enclosed; 42. post temporal canal, open/enclosed; 43. dorsal nasal canal, open/enclosed; 44. frontal and supraorbital canal, open/enclosed; 45. dorsal process of cleithrum, present/absent; 46. medial shelf of coracoid, large/small; 47. length medial pelvic wing, to tip/not; 48. width medial pelvic wing, broad/narrow; 49. post temporal canal, broad, shallow/narrow, deep; 50. infraorbitals, 3/less than 3; 51. epiotic crest, large/small.

or drought, streams decrease in runoff and refuge areas may dry out, so that the water becomes warmer, more saline, anoxic, or more acidic (Glover, 1982). The evolution of the smaller fishes appears to have entailed selection in favour of maintaining broad physiological adaptability. The tolerance of freshwater fishes to adverse conditions

has been discussed by Whitley (1945), Glover and Sim (1978a and b), Beumer (1979), and Glover (1979, 1982).

are possibly some of the best-known and best-studied of the small endemic fish.

PREVIOUS TAXONOMIC WORK

The lack of taxonomic work, particularly for the smaller endemic fish, has attracted comment from McDowall (1981) and Keast (1981). In many cases it is not known how many species actually exist within a particular genus. This lack of knowledge is being remedied, with work in progress for a number of families and genera. The atherinids and related blue-eyes and rainbowfishes, for example,

HYPOTHESES

In 1978, both Ivantsoff and Patten, working on atherinid systematics, advanced independent hypotheses regarding the origins of three distinct groups within the predominantly freshwater atherinid genus *Craterocephalus*.

Patten (1978) stated: "There is no doubt divergence between the "*eyresii*" and "*stercusmuscarum*" groups occurred in the coastal seas of the Australian mainland. Western Australia

TABLE 2. Thirty-nine characters used in Felsenstein's (1985) Bootstrap analysis. The characters are designated as primitive (P), medium (M) and advanced (-) based on work by Rosen and Parenti (1981), White (1985) and B. Said (pers. comm.).

1, vomerine teeth, present, primitive; 2, mesopterygoid teeth, present, primitive; 3, basibranchial toothplate, present, primitive; 4, 5th ceratobranchials unfused, primitive; 5, mesopterygoid large, primitive; 6, fewer infraorbitals, advanced; 7, large 3rd infraorbital, primitive; 8, epiotic crest large, primitive; 9, basihyal bone long, primitive (3 states); 10, basihyal cartilage small, primitive (3 states); 11, unciate process of 1st epibranchial large, primitive (3 states); 12, urohyal ventral pocket present, primitive; 13, urohyal ventral wings present, primitive; 14, posterior process urohyal long, primitive; 15, coracoid posterior edge without notch, primitive; 16, scapular foramen small, primitive; 17, anterior medial process of pelvic long, primitive; 18, ventral flange of 5th ceratobranchial small (low), primitive; 19, ventral flange 5th ceratobranchial not elongated, primitive; 20, number of interdorsal pterygiophores reduced, advanced; 21, interdorsal pterygiophores well developed, primitive (3 states); 22, anal plate reduced, primitive (3 states); 23, reduced numbers of epipleural ribs on caudal vertebrae, advanced; 24, mesethmoid present, primitive; 25, enlarged teeth on anterior of 5th ceratobranchial, primitive; 26, supraoccipital crest large, primitive; 27, narrow dermosphenotic, advanced; 28, large quadrate, primitive; 29, narrow ectopterygoid, primitive; 30, anterior projection of coronoid small, primitive; 31, cleithrum with dorsal process, advanced; 32, cleithrum dorsal process large, advanced; 33, cleithrum with anterior process, primitive; 34, supracleithrum long and slender, primitive; 35, infraorbital canal enclosed, primitive (3 states); 36, post temporal canal enclosed, primitive; 37, nasal canal enclosed, primitive; 38, frontal and supraorbital canals enclosed, primitive; 39, dorsal process of cleithrum rounded, primitive.

<i>C. s. fulvus</i>	---PP-PPP-PPPPPPPPPPMP--P--PP--P---P
<i>C. s. stercusmuscarum</i>	---PP-PPP-PPPPPPPPPP-P--P--PP--P---P
<i>C. dalhousiensis</i>	---PPPPMM-PPPPPMPPPP--P--PP--P---P
<i>C. randi</i>	---PPPPPP-PPPPPMPPPPMP--P--PP--P---P
<i>C. nouhuysi</i>	---PPPPPP-PPPPPPPPPP---P-PPP---PM--P
<i>C. lucustris</i>	---PP-PPM-PPPPPPPPPP---P--PP---P
<i>C. lentiginosus</i>	---PPPPPPPPPPPPPP-PPPPM--P--PP--P---P
<i>C. eyresii</i>	--P---P---P---MM--P-PPP--P---P
<i>C. cuneiceps</i>	--P---MM---M-MPP--P--PP-PPPPPP---P
<i>C. marjoriae</i>	--P---MM-----PP--P--PP--PM---P
<i>C. marianae</i>	--P-P-PPM-----P-PP-PPPPPP-P-M---
<i>C. helenae</i>	--P-P-PPM---M--PMPM-PPPP--P-PM---
<i>C. kailolae</i>	---P--P--P--P-M---P---PPP-P---PPPM
<i>C. honoriae</i>	PPPPPPPP--PPM--PM--PMM-----PP-P-----
<i>C. pauciradiatus</i>	--P--PPP--PM--P-PPPM---P-PP--P---P
<i>C. capreoli</i>	--PPPPPP--PM--PP--PMM---PPPP-P-M---
<i>C. mugiloides</i>	PPPPPPPP---PM--PM--PMP-P--P-PP-P-----

is the most likely dispersal centre since *Craterocephalus pauciradiatus* is found there and also *C. capreoli*, the most probable sister species of the combined "*eyresii*" and "*stercusmuscarum*" groups". However, he gave no indication of how or when these fish might have entered the freshwaters of Australia and Papua New Guinea.

Ivantsoff (1978) suggested: "It is possible that the marine ancestor of *Craterocephalus* had entered through Canning Basin and spread through epicontinental seas" (during the mid-Cretaceous). "As the seas withdrew it fragmented populations which eventually evolved into *C. cuneiceps* . . . *C. marjoriae* . . . , and *C. eyresii*". In addition he stated: "With the onset of Cretaceous the Great Artesian Basin and the Murray Basin became separated possibly providing a barrier which may have resulted in a new line leading to *Craterocephalus stercusmuscarum*, *C. lacustris* and *C. nouhuysi*."

My preliminary electrophoretic work suggests that members of the two freshwater species groups ("*eyresii*" and "*stercusmuscarum*") are so dissimilar genetically as to appear almost separate genera. As a result of this work, a third hypothesis may be presented as follows. Initial entry of the ancestral *Craterocephalus* species was from the N and NW, probably during the mid-Cretaceous (110-95 My) marine transgression when an epicontinental sea covered most of the mainland (Veevers, 1984). As the water regressed peripheral populations retreated with the marine/estuarine habitats. Other populations, isolated further inland, survived and gave rise to species in the "*eyresii*" group. Marine/estuarine populations reinvading during later marine transgressions (Oligocene/early Miocene), also from the N and NW, gave rise to the "*stercusmuscarum*" group.

MATERIALS AND METHODS

Wherever possible, osteological studies were made on at least two or three specimens of each species. Alizarin specimens were prepared using standard techniques developed by Taylor (1967). Results of observations were given binary values (1/0) for presence/absence, large/small (Table 1), or were coded as advanced/primitive (Table 2) following the works of Rosen and Parenti (1981), White (1985) and B. Said (pers. comm.). These values were used in two cluster analysis programmes. Analysis of binary values for 51 osteological characters used a procedure based on an algorithm from Sneath and Sokal (1973),

modified by Dr G.M. McKay (Macquarie University). The primitive/advanced characters (39) were used in the "bootstrap" method of Felsenstein (1985) which includes an hypothetical ancestor with primitive characters.

The study used cleared and stained specimens from the following institutions: AMS — Australian Museum, Sydney; MU — Macquarie University, Sydney; WAM — West Australian Museum, Perth. Other specimens from the MU collection: KB Field number — collected by Mr Keith Bishop; JMP Field number — collected by Patten (1978); LC Field number — collected by the author; WI Field number — collected by Dr W. Ivantsoff.

LIST OF SPECIMENS

Craterocephalus honoriae JMP 75-5 (5) Smiths Lake, N.S.W.

Craterocephalus mugiloides KB 75-35 (4) Roeburne, W.A.; KB 75-46 (10) Perth, W.A.; KB 75-32 (5) Port Hedland, W.A.; JMP 77-15 (6) Exmouth Gulf, W.A.; AMS 1A 6760 (1) Lindeman Island, Qld.

Craterocephalus capreoli WI 75-26 (1) Exmouth Gulf, W.A.; KB 75-32 (3) Port Hedland, W.A.

Craterocephalus pauciradiatus WI 309 (1) Cleaverville Creek, W.A.; WI 75-27 (3) Exmouth Gulf, W.A.

Craterocephalus eyresii WI 73-4 (3) Lake Bonney, S.A.; WI 70-52 (2) Peel River, N.S.W.; LC 84-1 (2) Warialda Creek, N.S.W.; LC 87-1 (2) Cockburn River, N.S.W.

Craterocephalus marjoriae JMP 77-5 (3) Tabulant, N.S.W.; MU 75-1 (1) Gayndah, Qld; JMP 75-76 (3) Gympie, Qld; LC 84-2 (2) Mary River, Imbil, Qld.

Craterocephalus marianae WI 78-1 (3) Magela Creek, N.T.

Craterocephalus helenae WAM P 25424-008 (2) Drysdale River, W.A.

Craterocephalus kailolae WAM P 17783-001 (3) Foasi Creek, Papua New Guinea.

Craterocephalus stercusmuscarum stercusmuscarum JMP 78-15 (1) Mackenzie River, Qld; JMP 75-70 (3) Mulgrave River, Qld; JMP 75-74 (2) Lotus Creek, Qld; WI 75-21 (2) Cairns, Qld.

Craterocephalus stercusmuscarum fulvus MU 70-22 (2), Manila, N.S.W.; JMP 75-39 (2) Lake Wabby, Fraser Island, Qld; JMP 75-60 (2) Goondiwindi, Qld; LC 84-3 (3) Mary River, Imbil, Qld.

Craterocephalus randi WI 70-41a (2); Fly River, Papua New Guinea.

Craterocephalus nouhuysi AMS 117319-001 (1)
Lorenz River, West Irian; WAM P 27806-005 (2)
Tabubil, PNG.

Craterocephalus lacustris WI 70-40c (7); WAM P
28159 002 (3), Lake Kutubu, PNG.

Craterocephalus lentiginosus WAM P 25029 003
(2) Prince Regent River, W.A.

Craterocephalus dalhousiensis WI 76-6 (7)
Dalhousie Springs, S.A.

RESULTS

The three species groups identified by Ivantsoff (1978) and Patten (1978), namely "*eyresii*", "*stercusmuscarum*" and "*honoriae*", are now more clearly defined. Further species belonging to the first two groups have recently been described (Ivantsoff *et al.*, 1987a & b; Crowley & Ivantsoff, 1988).

The results of the cluster analyses (Figs 1 and 2) show that the "*stercusmuscarum*" group is more closely aligned with the "*honoriae*" group than it is with the "*eyresii*" group. Evidently the divergence between the first two groups was later than that between the two freshwater groups ("*eyresii*" and "*stercusmuscarum*").

In Figure 1 *C. s. stercusmuscarum* and *C. s. fulvus* cluster together and *C. randi* is close to this pair. The similarity between these fish suggests clinal variation rather than true specific differences, but there are minor morphological differences by which they may be recognized. *Craterocephalus marjoriae* and *C. marianae*, which previously were not recognized as separate species (see Ivantsoff *et al.*, 1987a), also cluster together, although there are

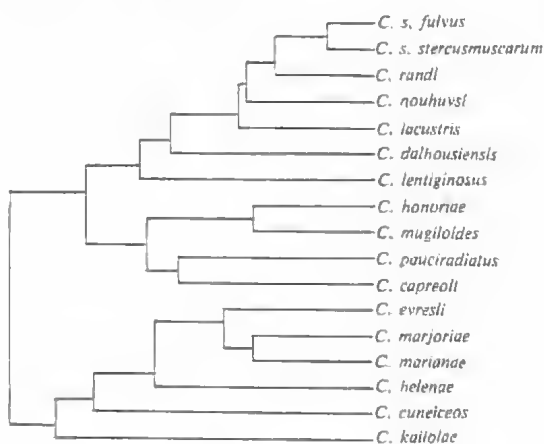


FIG. 1. Cluster analysis of *Craterocephalus* species using an algorithm based on Sneath and Sokal (1973).

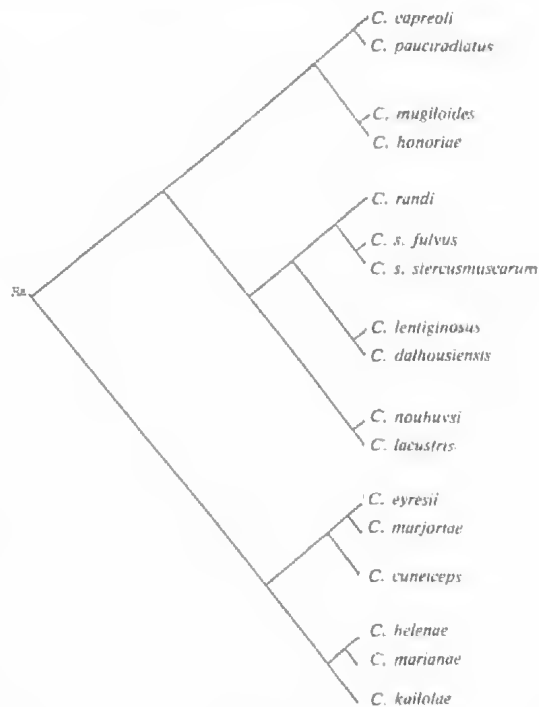


FIG. 2. Cluster analysis of *Craterocephalus* species based on the "bootstrap" method of Felsenstein (1985). Ha, hypothetical ancestor.

major osteological differences between them. For example, *C. marianae* has well-developed interdorsal pterygiophores whereas *C. marjoriae* has none (or one or two vestiges at most). In this cluster analysis these two species are most closely aligned with *C. eyresii*.

Although there are slight differences between the cluster analyses in Figures 1a and b, *C. dalhousiensis* and *C. lentiginosus* cluster together in both, as do *C. lacustris* and *C. nouhuysi*, the two species from the Highlands of Papua New Guinea and Irian Jaya. From the second analysis it is apparent that the "*honoriae*" and "*stercusmuscarum*" group are the same lineage whereas the branch leading to the "*eyresii*" group leads directly from the point of hypothetical ancestry. This is reflected in the cluster analysis (Fig. 1) where the "*honoriae*" and "*stercusmuscarum*" groups arise from the same branch even though no hypothetical ancestor is invoked.

DISCUSSION

The clustering of the (freshwater) "*stercusmuscarum*" group with the (marine)



FIG. 3. Distribution of *Craterocephalus* species. Areas of sympatry between "eyresii" and "stercusmuscarum" species are shown by cross hatching. Open circles, "stercusmuscarum" species; closed squares, "eyresii" species.

"honoriae" group in both analyses indicates that divergence between these two was probably later than the divergence of either from the "eyresii" group. These results support, but do not prove, the hypothesis of two separate invasions into freshwaters of Australia. Osteological differences are more apparent between some species of the "eyresii" group (e.g. *C. kailolae*, *C. marjoriae* and *C. marianae*; see Ivantsoff *et al.*, 1987b; Crowley & Ivantsoff, 1988) than between any species of the "stercusmuscarum" group. These differences imply more recent speciation in the latter group and a longer period of separation from the hypothetical ancestor for the "eyresii" species. The osteological differences are reflected in electrophoretic work presently being carried out, and again the results suggest the possibility of two separate invasions of hardyheads into Australian freshwaters.

DISTRIBUTION, DISPERSAL AND BIOGEOGRAPHY

If the distribution of the two freshwater groups is examined (Fig. 3), sympatry is found between

members of both groups throughout parts of the range in eastern and northern Australia. In the Murray/Darling drainage system *C. eyresii* and *C. s. fulvus* ("stercusmuscarum") may be sympatric whereas in the rivers of southeastern Queensland, *C. s. fulvus* is sympatric with *C. marjoriae* (a member of the "eyresii" group). In the Northern Territory, *C. marianae* ("eyresii" group) and *C. s. stercusmuscarum* are sympatric. Sympatry of *C. stercusmuscarum* with three species of the "eyresii" group in different areas (two of which are contiguous), again suggests a longer period of separation allowing for speciation in the latter ("eyresii") group.

Craterocephalus randi and *C. nouhuysi* may be sympatric in Papua New Guinea (Upper Fly River), where only members of the "stercusmuscarum" group are present in the southern drainages. Osteologically, *C. nouhuysi* is the most distinct of the "stercusmuscarum" group whilst *C. randi* is almost indistinguishable from *C. s. stercusmuscarum*. *Craterocephalus randi* may have been in contact with species of northern mainland Australia as recently as 7-10,000 years ago, during the last glacial period (which would account for the close similarity with *C. stercusmuscarum* both osteologically and morphologically); the two other species from the Highlands of Papua New Guinea, *C. lacustris*, and *C. nouhuysi*, have possibly been separated from the main "stercusmuscarum" population since the uplifting of the Highlands in the Oligocene/Miocene (Dow, 1977; Pigram & Davies, 1987). In the northern drainages of Papua New Guinea a single very distinctive species, most closely aligned with the "eyresii" group, is the only hardyhead known (Ivantsoff *et al.*, 1987b).

If the distribution of some members of both groups is examined in more detail, and with regard to the geologic history of Papua New Guinea and Australia, it becomes evident that Whitley's (1959) suggestion of recent origin cannot be valid. For example, *C. cuneiceps*, a member of the "eyresii" group, appears to have a disjunct distribution: it is found in the coastal rivers of Western Australia, and a morphologically similar fish (also similar in many respects to *C. eyresii*) is found in the Finke River of central Australia. While the region between these areas once had numerous rivers, some of which flowed eastward to the centre, there has been no continuous connection — either freshwater or brackish — since mid-Miocene times (van de Graaff *et al.*, 1977). Even during times of flood, when some of the prior lakes and streams of the region are again in evidence, there is still no evidence of connection. Although aligned with *C.*

cuneiceps, to which it appears morphologically and osteologically most similar, the identity of this central Australian fish is equivocal. Even though future studies may prove it to be a different species, the relationship between this fish and *C. cuneiceps* is very close, despite the possible 12-15 million years of separation.

Similarly, *C. eyresii* has a disjunct distribution: it is present in South Australia, and an osteologically-similar fish exists in the Murray/Darling drainages and the Goulburn/Hunter River system on the E coast of New South Wales. In the last case, river capture of the previously westward-flowing headwaters of the Goulburn River (in late Oligocene/early Miocene times; Galloway, 1967; Wellman & McDougall, 1974) is suggested to account for the eastern population. Alternatively, this population, as well as other small species (e.g. retropinnids), might somehow have reached the Hunter River more recently. Complete disjunction between the South Australian and Murray/Darling populations has not been proven, as fish may possibly still move between the two drainages in times of exceptional floods. If such exchanges are not possible, then these populations of *C. eyresii* would have had no contact since the uplifting of the Flinders Ranges and diversion of the Murray River (see Veivers 1984, p. 143-9).

Excepting the possibility of *C. eyresii* and some other small species finding their way over the Liverpool Range, or between the Murray/Darling Drainage System and the Lake Eyre Drainage, the length of time indicated in these two cases (*C. cuneiceps*, *C. eyresii*) suggests that speciation in *Craterocephalus* has not been rapid.

In the "*stercusmuscarum*" group, *C. dalhousiensis* is found in a very restricted habitat which has only been in existence since Plio-Pleistocene times (5-2 My; Krieg, 1984). Osteologically it is closest to *C. lentiginosus* (Figs 1 & 2) which is found in the Fitzroy and Prince Regent Rivers, southern Kimberleys, and, as mentioned previously, there has been no water connection between these areas since the mid-Miocene (van de Graaff *et al.*, 1977). However, the habitat of *C. dalhousiensis* is the very warm waters of the mound springs at Dalhousie (Ivantsoff & Glover, 1974) and it is possible that adaptation and speciation occurred fairly rapidly in such an unusual environment.

The distribution of *C. s. fulvus* in the Murray/Darling System, as well as in the southeastern coastal rivers of Queensland, suggests that this fish must have been present in these areas

before the eruption of the Tweed volcanic shield, about 20-23 My (Wellman & McDougall, 1974). This, too, implies that the "*stercusmuscarum*" group also is not of "recent" origin.

Divergence between *C. eyresii* and *C. marjoriae*, with which *C. s. fulvus* is sympatric, probably occurred before the Miocene eruptions, and possibly during earlier tectonic instability of this region (Webb *et al.*, 1967). McCulloch (1914), in discussing the distribution of Murray Cod and Australian Perch in NE New South Wales and SE Queensland (similar to the distribution of *C. eyresii*, *C. marjoriae* and also *C. s. fulvus*), suggested that there could have been recent separation of the headwaters of the rivers in that area from those of the northern Darling River System. However, Stuart Rowland (pers. comm.) has found genetic differences between the eastern and western populations of Murray Cod. These differences suggest either that the Murray Cod is a recent but less genetically conservative species than *C. s. fulvus* (which has remained as a single species), or that it has been sympatric with the two "*eyresii*" group species for a longer period of time. In either case, speciation can hardly be of recent origin for any of these fish.

In northern Queensland *C. s. stercusmuscarum* is found in rivers on both sides of the Eastern Highlands. These highlands date from Miocene to late Pleistocene (Wyatt & Webb, 1970; Wellman, 1978, 1987; Coventry, 1980), and yet the hardyhead populations on either side are identical. This leads to the conclusion that either the hardyheads have recently entered these rivers from marine environments on both sides (Gulf of Carpentaria and Coral Sea) or there has been insufficient time for speciation to have occurred since the eastern and western flowing rivers were separated (Hopley *et al.*, 1980).

More unusual mechanisms have also been invoked to account for the present distribution of freshwater fishes in Australia. Rains of fishes have been documented (Whitley, 1959), and it is possible that some fish carried by water-spouts may be dropped in new and suitable habitats. The members of the Horn Scientific Expedition (1896) found fish in man-made bores at both Coward and Strangeways Springs in South Australia, and suggested that these may have been introduced as eggs on the feet or feathers of birds (see also Whitley, 1945). Presumably this latter mechanism would apply only to eggs which had adhesive filaments or could adhere to the birds in some other way. By comparison it seems more probable that much of the present distribution of freshwater

fishes has resulted from dispersal in floodwaters coupled with the effects of past geologic events, as suggested by McDowall (1981).

The recent increase in taxonomic work has shown that there are many more species than were recognized when Whitley (1959), McDowall (1981), Keast (1981), and Talent (1984) wrote on the biogeography of Australian fishes. Much of the previous biogeographic work concerned the global affinities of the Australian ichthyofauna. McCulloch (1914) discussed the relationships of Australian galaxiids to those in other southern continents and islands, and also mentioned the "Antarctic Continent" theory (but unfortunately gave no reference for this quote). He also discussed the similarities of some marine fish to those of New Zealand, and to some extent South Africa, and the distribution of Australian marine fishes along the east coast. Haswell (1914) likewise discussed the affinities of galaxiids and also of the lungfish *Neoceratodus*.

The biogeography and affinities of Australian fish compared with those from other continents has been under review since late last century (see McDowall, 1981). However, the biogeography of freshwater fish within the continent has not previously been examined in detail, although the distribution has been discussed by some authors (e.g. McDowall, 1981; Merrick & Schmida, 1984).

Rosen (1964) proposed that atherinids could have originated in the brackish waters of Australia. If this were the case, then the family must be very old, since atherinids of Eocene age have been described from France (Chedhomme & Gaudant, 1984). Consequently Rosen's proposal would imply that atherinids dispersed from the Australian region before the Eocene. In its osteology the French Eocene atherinid, *Palaeoatherinia formosa*, is almost identical to the extant genus *Atherinomorus* (= *Pranesus*), although some of its characters appear more primitive (e.g. position of pectoral girdle). An alternative speculation is that atherinids may have originated in the Tethys Sea and come to the Australian region from there. Forman and Wales (1981) mentioned Tethyan influences in mid to Late Cretaceous fossil material from the Canning Basin and suggested that a warm current could have brought the Tethyan fauna to that region. Ancestral atherinids might also have come by this route and spread throughout the mid-Cretaceous Australian epicontinental sea.

As an alternative to mid-Cretaceous entry, initial invasion may have been via a southern route through the Eucla and Murray Basins during Late Cretaceous or Early Paleocene times, when

separation of Australia and Antarctica may have occurred (Cande & Mutter, 1982). A second invasion may have taken place, as previously proposed, with speciation occurring between then and Late Miocene/Early Pleistocene. But if Forman and Wales (1981) are correct in recognising Tethyan influences in the Canning Basin, and, acknowledging the conservatism of the family through time from the meagre atherinid fossil record available, the earlier initial invasion does appear plausible.

Although Whitley (1959) and later authors (e.g. Allen & Cross 1982; Merrick & Schmida 1984) considered the freshwater fishes of Australia to be of recent origin, I suggest that despite the present lack of atherinid fossils in Australia (see, for instance, Turner, 1982), hardyheads at least (and most probably rainbowfishes with similar species distributions) are not the result of recent speciation. The existence of modern-looking fossil atherinids in the Eocene of France (Chedhomme & Gaudant, 1984) and the Pleistocene of Arizona, where fossils of an extant species have been found (Todd, 1974), indicate that atherinids are very conservative and that speciation is unlikely to have been rapid in this family.

It appears that the relative tectonic stability of Australia, combined with climatic conditions and the physiological adaptability of many of the small endemic fish, have been the major factors influencing speciation (or lack of it) in those fish families which have survived and are endemic to Australian freshwaters. Given these conditions, and the lack of large, permanent water bodies, it is not surprising that the Australian freshwater fish fauna appears depauperate when compared with that of South America or of Africa.

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